

## Research Paper

**Cite this article:** El-Keblawy A, Al-Shamsi N, Mosa K (2018). Effect of maternal habitat, temperature and light on germination and salt tolerance of *Suaeda vermiculata*, a habitat-indifferent halophyte of arid Arabian deserts. *Seed Science Research* **28**, 140–147. <https://doi.org/10.1017/S0960258518000144>

Received: 8 December 2017

Accepted: 6 April 2018

**Key words:**

arid deserts; dark inhibition; germination recovery; germination response; seed dormancy; time of germination

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# Effect of maternal habitat, temperature and light on germination and salt tolerance of *Suaeda vermiculata*, a habitat-indifferent halophyte of arid Arabian deserts

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**Abstract**

Habitat-indifferent species that can grow well in both saline and non-saline soils offer a good opportunity for studying seed dormancy and salt tolerance during germination. Here, we assess interactive effects of maternal habitat and incubation conditions on salt tolerance during germination of the habitat-indifferent halophyte *Suaeda vermiculata*, a common perennial shrub of the arid Arabian deserts. Seeds collected from saline and non-saline habitats were germinated at six salinity levels (0–500 mM NaCl) and incubated at three temperatures and under two light regimes. Studied germination attributes were final germination, germination rate index (GRI) and germination recovery of non-germinated seeds when transferred to distilled water. The results showed insignificant difference in salt tolerance between seeds of the two habitat types at the lower salinities. At higher salinities (400 and 500 mM NaCl), germination of the saline habitat seeds was almost inhibited, but that of non-saline habitat seeds reached various levels depending on light and temperature. Both higher temperatures and darkness resulted in significant reductions of the final germination at the higher salinities. Seeds of the two habitats that did not germinate in the different treatments recovered their germination when transferred to distilled water, indicating that these seeds maintained their viability in saline solution and were able to germinate upon the arrival of suitable conditions. Seeds of the two habitats germinated within 2 days at the lower salinities and GRI decreased with the increase in salinity level. Such reduction was obvious for seeds of the saline habitat. Recovery was faster for seeds of the saline habitats, especially for those incubated at higher salinities and in the dark. The difference in dormancy and germination attributes of seeds of the two habitat types reflects ecological adaptations for survival in salt marshes of arid deserts.

**Introduction**

Excessive increases of salts in soil severely reduce the most critical stages in the life cycle of plants, especially germination and seedling growth and survival (Greenway and Munns, 1980). Seed tolerance to salinity is usually interpreted as the ability of seed to germinate at high salinities, and to recover their germination after transfer from saline to non-saline solutions (Ungar, 1995). Under salt stress, embryo growth is restricted due to osmotic stress, ionic toxicity, oxidative stress and nutrient imbalance (Grattan and Grieve, 1998). Several studies have indicated that the negative effect of salinity on seed germination is through a decrease in soil water potential, so that seed imbibition is compromised, and/or by excessive entry of Na<sup>+</sup> which is toxic to metabolism (Kranner and Seal, 2013; Hameed *et al.*, 2014). Uptake of salts could lower the seed's water potential, thus facilitating imbibition; however, ionic toxicity may overshadow such beneficial osmotic effects (Gul *et al.*, 2013).

Seeds of desert plants use environmental and hormonal signals as sensors for detecting the proper environmental conditions that could trigger germination when the environments are suitable for seedling growth and survival (El-Keblawy and Gairola, 2017). Temperature and light are important environmental signals that can modulate time of seed germination (Benech-Arnold *et al.*, 2000). The response of seeds to light as an environmental signal, may be a genetic characteristic or modulated by maternal habitats and is mediated by phytochrome (Jones and Hall, 1979). In addition, light may interact with temperature and salinity to determine the timing of germination in seeds of several halophytes (Qu *et al.*, 2008; Gul *et al.*, 2013). Despite such extensive knowledge on germination requirements of seeds of true

halophytes, few studies have assessed the salinity, temperature and light requirements for seeds matured in saline and non-saline habitats of habitat-indifferent halophytes.

Transgenerational induction has been defined as the change in offspring phenotype that is cued by an environmental signal in the parental generation, and is expressed independently of changes in the offspring genotype (Holeski *et al.*, 2012). Transgenerational mechanisms may occur through maternal and/or epigenetic effects. In maternal effects, progeny phenotypes are altered as a function of the environment created by or experienced by the maternal parent (Donohue, 2009). Maternal effect is adaptive when it enhances offspring fitness in an environment similar to that experienced by the parental generation (Rossiter, 1996, 1998; Donohue and Schmitt 1998). Several studies have reported that seed dormancy and germination requirements of the same species differ depending on maternal habitat and time of seed development on the mother plant (Fenner, 1991; Wulff, 1995; Gutterman, 2000; El-Keblawy *et al.*, 2017a,b). Adaptive maternal effects are expected to be evolved as mechanisms to ameliorate factors that reduce plant fitness under certain stress factors (Galloway, 2005). For example, maternal effect has been proposed to ameliorate drought stress in *Impatiens capensis* (Maruyama *et al.*, 2016) and *Thymelaea hirsuta* (El-Keblawy *et al.*, 1996), and salinity stress in *Anabasis setifera* (El-Keblawy *et al.*, 2016) and *Suaeda aegyptiaca* (El-Keblawy *et al.*, 2017a).

*Suaeda vermiculata* is a habitat-indifferent halophyte of the Arab Gulf deserts (i.e. it can grow very well in both saline and non-saline habitats; Cushman, 2001). It produces very tiny seeds (see Supplementary material 1) with no dispersal structures. Species with limited seed dispersal experience generations of selection by local environmental conditions (Galloway and Etterson, 2009). The presence of multiple generations of habitat-indifferent halophytes within a single environment would increase the likelihood of germination differentiation between saline and non-saline environments (Moriuchi *et al.*, 2016). The aim of this work was to assess salt tolerance of *Salsola drummondii* in response to maternal habitat, and temperature and light of incubation. The study also aimed to assess the effect of maternal habitat and temperature of incubation on the ability of *S. vermiculata* seeds to recover their germination in distilled water after being exposed to saline solutions. We hypothesized that exposure of multiple generations of the saline habitat to salinity stress helps their seeds to tolerate higher salinity stress during germination, compared with seeds from plants of non-saline habitats that have not previously been exposed to any salinity stress.

## Materials and methods

### Study species

*Suaeda vermiculata* is a leaf succulent perennial shrub growing in both saline and non-saline habitats of the Arab Gulf deserts. The average mass of seeds collected from the saline habitat was significantly heavier (0.447 mg) than that of seeds from the non-saline habitat (0.153 mg). However, there was no significant difference in the viability between the seeds of the two habitats (97.6 and 96% for seeds of the non-saline and saline habitats, respectively; see Table 1). The associated species with *S. vermiculata* give a preliminary idea about the salinity levels of the two habitats. Both habitat types have habitat-indifferent halophytes that can grow well in both saline and non-saline habitats (e.g. *Salsola*

*drummondii*, *Zygophyllum qatarense* and *Aeluropus lagopoides*). However, the saline habitat has true halophytes (e.g. *Halopeplis perfoliata* and *Halocnemum strobilaceum*), but the non-saline habitat has glycophytes (e.g. *Launaea capitata*, *Pennisetum divinum*, *Cornulaca monacantha* and *Indigofera oblongifolia*; see Supplementary material 1).

## Study site and seed collection

### Soil attributes

Soil of the saline habitat was sandy with high ratios of silt and clay and sometimes hard gypsum, especially during the dry season (i.e. summers and autumns). However, soil of the non-saline habitat was sandy with a high proportion of small gravels. Both salinity and electric conductivity (EC) were significantly greater in saline (5.86 g l<sup>-1</sup> and 18.49 mS cm<sup>-2</sup>, respectively) than in non-saline habitat (0.36 g l<sup>-1</sup> and 1.62 mS cm<sup>-2</sup>, respectively). However, there was no significant difference in soil pH between the two habitat types (Table 1).

### Climate

The Northeast region of the United Arab Emirates (UAE) is hot and dry with a sub-tropical arid climate. The climatic data of the study area, based on 30-year records (1885–2015) of the nearest meteorological station in Fujairah, indicates that the coolest month is January (maximum and minimum temperatures are 24.0 and 16°C, respectively), while the hottest months are June and July (maximum and minimum temperatures are 40.0 and 30°C, respectively). The average amount of annual rainfall is about 110 mm with extreme variability in space and time, and most of the rainfall occurs from November to March, when average temperatures are lowest (Merabtene *et al.*, 2016). The average relative humidity ranges from 45% in May to 67% in August. The daily mean temperature ranges between 12.1°C in January and about 42°C in June–August, and can reach up to 48°C in summer. The average annual rainfall in the coastal area is 120 mm (Böer, 1997).

### Seed collection

Mature seeds of *S. vermiculata* were collected from two sites around Kalba city, on the northeast coast of the UAE, during January 2015 (two weeks after first effective rainfall). The first site was a salt marsh (24°99'68.68" N and 56°34'91.90" E) and the second was a non-saline gravel plain (25°02'94.17" N and 56°36'17.56" E). Seeds were randomly collected from the whole population to represent its genetic diversity. Immediately after collection, seeds were air dried and threshed to separate debris by using a hand-made rubber thresher. Seeds were cleaned and stored in brown paper bags at room temperature (22 ± 2°C) until their use in the germination experiment in April 2016. The seed mass was determined by weighing three batches, each containing 100 seeds, from both saline and non-saline habitats.

In both saline and non-saline habitats, five soil samples were collected from around the roots of *S. drummondii* and used for testing EC and pH. Soil samples were air dried and sieved before use in the analyses. Soil salinity, EC and pH were measured from a 1:5 soil:water suspension (Dahnke and Whitney, 1988).

**Table 1.** Comparison between seed and habitat characteristics of *Suaeda vermiculata* seeds in saline and non-saline habitats. EC and pH were determined in a 1:5 water extract

Parameter	Non-saline habitat	Saline habitat	Two-samples <i>t</i> -test	<i>P</i>
Seed mass (mg)	0.153	0.447	5.167	<0.001
Seed viability (%)	97.6	96.0	0.79	0.493
pH	8.133	8.233	0.35	0.743
Salinity (g l <sup>-1</sup> )	0.361	5.86	19.492	<0.001
EC (mS cm <sup>-1</sup> )	1.620	18.490	9.224	<0.001
Associate species	<i>Salsola drummondii</i> , <i>Salsola imbricata</i> , <i>Cornulaca</i> sp., <i>Aerva javanica</i> , <i>Indigofera</i> <i>oblongifolia</i> , <i>Launea capitata</i>	<i>Salsola drummondii</i> , <i>Aeluropus lagopoides</i> , <i>Halopeplis perfoliata</i> , <i>Halocnemum strobilaceum</i> and <i>Zygophyllum qatarense</i>		

### Effect of maternal habitat on germination response to salinity, light and temperature

To assess the impact of maternal habitat on response of *S. vermiculata* seed germination to salinity, light and temperature of incubation, seeds of both saline and non-saline habitats were germinated at six salinity levels (0, 50, 100, 200, 400 and 500 mM NaCl) in three incubators adjusted to three temperatures and two light regimes. The three temperature regimes consisted of day/night cycles of 25/15, 30/20 and 35/25°C, where high temperature coincided with 12 h of white light. The light regime was 12 h light/12 h dark, or continuous dark, hereafter referred to as light and dark. The provided light was cool white fluorescent light with an intensity of 960 μmol m<sup>-2</sup> s<sup>-1</sup>. The used salinity levels were selected based on the results of a preliminary experiment assessing salt tolerance in *S. drummondii*.

Seeds were germinated in 9-cm Petri dishes on a layer of Whatman no.1 filter paper, moistened with 10 ml of the test solutions. The dishes were wrapped with parafilm to minimize evaporation. During the dark treatment, dishes were wrapped in aluminum foil to prevent any exposure to light. For each treatment, four replicates of 25 seeds each were used. Radicle emergence was the germination criterion and the number of germinated seeds was counted every other day for 20 days following seed soaking. Seeds incubated in the dark were counted only after 20 days. The viability of three batches of both saline and non-saline habitat seeds, each of 100 seeds, were tested for their viability using 1% (w/v) 2,3,5-triphenyl-tetrazolium chloride solution (Bradbeer, 1998).

### Germination recovery

After 20 days following seed soaking, all seeds that failed to germinate in different NaCl solutions under both the light and dark treatments were transferred to distilled water. The seeds were incubated again in light at the same temperature regimes as mentioned above. Germinated seeds were counted and removed daily for 10 days. Seeds of both saline and non-saline habitats that failed to recover were further tested for their viability using 1% (w/v) 2,3,5-triphenyl-tetrazolium chloride solution (Bradbeer, 1998). Three seed batches from each habitat type, each with 50 seeds, were used in this test.

### Data calculation and statistical analysis

The rate of germination was estimated by using a modified Timson index of germination velocity  $\Sigma G/t$ , where *G* is percentage

of seed germination at 2-day intervals, and *t* is total germination. The higher the value, the more rapid the germination. Germination rate was only calculated for seeds incubated under light conditions.

The germination recovery percentage was calculated by the following formula: Recovery percentage =  $[(a - b)/(c - b)] \times 100$ , where *a* is the total number of seeds germinated after being transferred to distilled water, *b* is the total number of seeds germinated in saline solution, and *c* is the total number of seeds. The rate of germination was also calculated using the modified Timson index of germination velocity (as above) to estimate the speed of the germination recovery.

Relative light germination (RLG) expresses the light requirement for seed germination and was calculated according to Milberg *et al.* (2000) by dividing the germination percentage recorded in the light by the sum of the germination percentages observed in light and in darkness. The values vary from 0 (germination only in dark conditions) to 1 (germination only in light).

Four-way ANOVAs were used to assess the significance of the main factors (maternal habitat, salinity, temperature and light) and their interactions on final germination, germination recovery, total germination (germination in saline solution + recovery germination) and germination rate index (GRI) during the recovery process. Three-way ANOVA was used to assess the impact of maternal habitat, salinity and temperature and their interactions on the GRI. Two-sample *t*-tests were used to assess the significance of the difference in soil EC, pH, salinity, seed mass and seed viability between saline and non-saline habitats. Tukey's test (honestly significant differences, HSD) was used to estimate the least significant range between means. The GRI was log-transformed and germination percentages were arcsine-transformed to meet the assumptions of ANOVA. This transformation improved the normality of the distribution of the data. All statistical methods were performed using SYSTAT, version 13.0.

## Results

### Germination in saline solutions

#### Effects on final germination

All the main factors (maternal habitat, salinity, temperature and light) and their interactions had significant effects on final germination of *S. vermiculata* seeds ( $P < 0.05$ , Table 2). The significant interaction between maternal habitat and salinity

**Table 2.** Results of four-way ANOVA showing the effects of maternal salinity, factors during incubation (salinity, temperature and light) and their interactions on final germination (i.e. germination in saline solutions), germination recovery, total germination (i.e. germination in saline solutions plus germination recovery) and germination rate index (GRI) during recovery of *Suaeda vermiculata* seeds

Source of variation	d.f.	Final germination		Total germination		d.f.	Recovery germination‡		GRI for germination recovery‡	
		Mean squares	F-ratio	Mean squares	F-ratio		Mean squares	F-ratio	Mean squares	F-ratio
Maternal salinity (MS)	1	8.726	855.6***	0.079	2.344	1	4.064	46.7***	93.9	30.6***
Salinity (S)	5	13.252	1299***	0.382	11.39**	4	9.405	108.1***	210	68.5***
Temperature (T)	2	1.929	189.2***	0.429	12.79**	2	0.270	3.10*	6.23	2.035
Light (L)	1	2.682	262.9***	0.275	8.21**	1	3.682	42.3***	14.2	4.7*
MS × S	5	0.752	73.7***	0.358	10.68***	4	0.322	3.70**	9.14	2.98*
MS × T	2	0.035	3.44*	0.009	0.275	2	0.110	1.267	1.622	0.530
MS × L	1	0.563	55.18***	0.043	1.271	1	0.896	10.31**	0.34	0.110
S × T	10	0.215	21.04***	0.110	3.28**	8	0.262	3.02***	3.73	1.217
S × L	5	0.083	8.12***	0.101	3.03*	4	0.690	7.93***	2.38	0.779
T × L	2	0.184	18.0***	0.112	3.34*	2	0.917	10.54***	8.15	2.661
MS × S × T	10	0.241	23.6***	0.074	2.21*	8	0.124	1.430	5.36	1.749
MS × S × L	5	0.170	16.7***	0.065	1.944	4	0.283	3.25**	13.3	4.251
MS × T × L	2	0.277	27.2***	0.071	2.131	2	0.191	2.194	0.48	0.158
S × T × L	10	0.059	5.8***	0.030	0.885	8	0.194	2.24*	1.47	0.481
MS × S × T × L	10	0.042	4.12***	0.090	2.70*	8	0.083	0.949	5.45	1.793
Error	216	0.010		0.033		180	0.087		3.06	

\* $P < 0.05$ , \*\* $P < 0.01$ , \*\*\* $P < 0.001$ . ‡Distilled water (0.0 NaCl) has been excluded from the analysis, as there was no recovery in this treatment.

( $P < 0.001$ ) indicates that the two habitats differ in their response to the different levels of salinity. Whereas no significant difference was detected between the seeds of the two habitats at the lower salinities, seed from the non-saline habitat tolerated more salinity, compared with those of saline habitat, at the higher salinities. For example, 28.7 and 7.7% of the non-saline seeds germinated in 400 and 500 mM NaCl, respectively, but less than 1% of the saline habitat seeds germinated in the same salinities (Fig. 1).

The interaction between maternal habitat and salinity and temperature of incubation was significant ( $P < 0.001$ , Table 2), indicating that salt tolerance of seeds of the two habitat types depends on the temperature of incubation. Seeds from the non-saline habitat germinated in all salinities (up to 500 mM NaCl) at 15/25 and 20/30°C, but only in up to 300 mM NaCl at 25/35°C. Seeds from the saline habitat, however, germinated only up to 300 mM NaCl at 15/25 and 20/30°C, but only up to 200 mM NaCl at 25/35°C (Fig. 1). The results also indicate that salt tolerance of seeds of the two habitat types responded differently to light; the interaction between maternal habitat and salinity and light was significant ( $P < 0.001$ , Table 2). Seeds from the non-saline habitat tolerated higher salinities (400 and 500 mM NaCl) in light, but not in darkness; in these salinities final germination of the non-saline seeds was 50 and 12.1% in light, but 7.4 and 3.4% in dark. Seeds of saline habitats displayed almost no germination in 400 and 500 mM NaCl (Fig. 1).

Germination of seeds of the non-saline habitat was neutrally photoblastic (RLG = 0.5) in 0.0, 100 and 200 mM NaCl at all temperatures, but was positively photoblastic in higher salinities. RLG was 0.6, 0.9 and 0.8 in 300, 400 and 500 mM NaCl, respectively, at 15/25°C and 0.6 and 0.8 in 300 and 400 mM NaCl, respectively, at

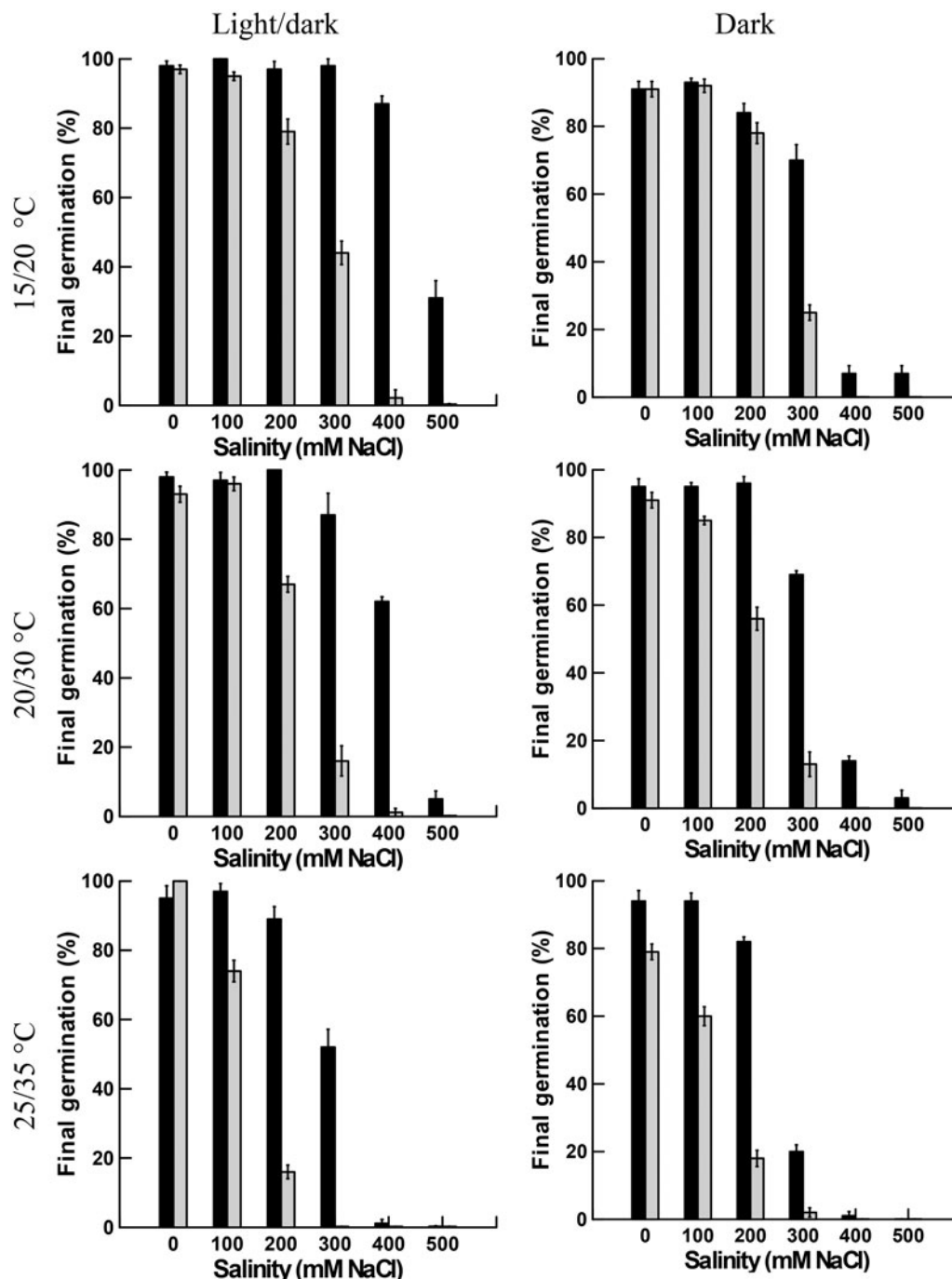
20/30°C and 0.7 at 300 mM NaCl at 25/35°C (RLG was calculated only when total germination of light and darkness was  $\geq 10\%$ ). For seeds from the saline habitat, however, it seemed that light was not an important factor controlling seed germination; RLG ranged between 0.5 and 0.6 with little variations among salinity levels and temperature (Fig. 1)

#### Effects on germination rate

There were significant effects for maternal habitat, salinity and temperature of incubation and all of their interactions (except for the interaction between maternal habitat and temperature) on GRI of *S. vermiculata* ( $P < 0.05$ ). Seeds of the two habitats attained a very fast germination at low salinities (0.0 and 100.0 mM NaCl); most seeds germinated within the first 2 days (GRI > 45). There was an insignificant difference in GRI between the seeds of the two habitats in the lower salinity levels (0, 100 and 200 mM NaCl) at the different temperatures. However, GRI of non-saline habitat seeds was faster, compared with that of saline habitat seeds, at higher salinities ( $\geq 300$  mM NaCl, Fig. 2).

#### Germination recovery

All the main factors and many of their interactions had significant effects on germination recovery of non-germinated seeds when they were transferred from the different salt solutions to distilled water ( $P < 0.05$ , Table 2). Interestingly, seeds that attained lower germination in the saline solutions had a higher recovery, indicating that the seeds of the two habitats did not lose their viability in the saline solutions.



**Fig. 1.** Effects of maternal salinity, and environmental factors during seed incubation (salinity, temperature and light) on final germination percentage (mean  $\pm$  SE) of *Suaeda vermiculata* seeds. Dark and light bars are for seeds of non-saline and saline habitats, respectively.

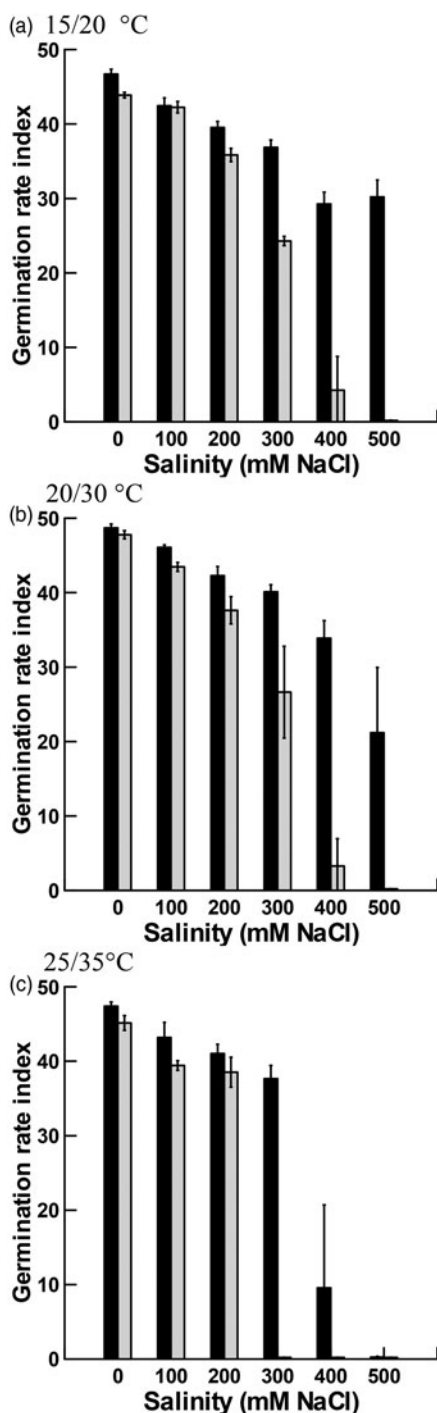
The interactions between maternal habitat, salinity and light had significant effects on germination recovery ( $P < 0.05$ , Table 2). Germination recovery in dark did not differ significantly between seeds of the saline and non-saline habitats in all salinities up to 400 mM NaCl. In light, however, recovery was significantly greater in seeds from the saline habitat, compared with that of non-saline habitat, in all salinities (Fig. 3).

The effect of the interaction between maternal habitat, temperature and light of incubation on germination recovery was significant ( $P < 0.05$ , Table 2). There was no significant difference in germination recovery between seeds of saline and non-saline

habitats incubated in light at the different temperatures. For seeds recovered from salinity and dark incubation, however, seeds of the saline habitats recovered to significantly higher levels at 15/25 and 20/30°C (58 and 62%, respectively) than seeds of non-saline habitat (22 and 36%, respectively).

#### Total germination

The impact of maternal habitat on total germination (i.e. in saline solution and after recovery) was insignificant ( $P < 0.05$ , Table 2), indicating that the greater germination of seeds from the non-

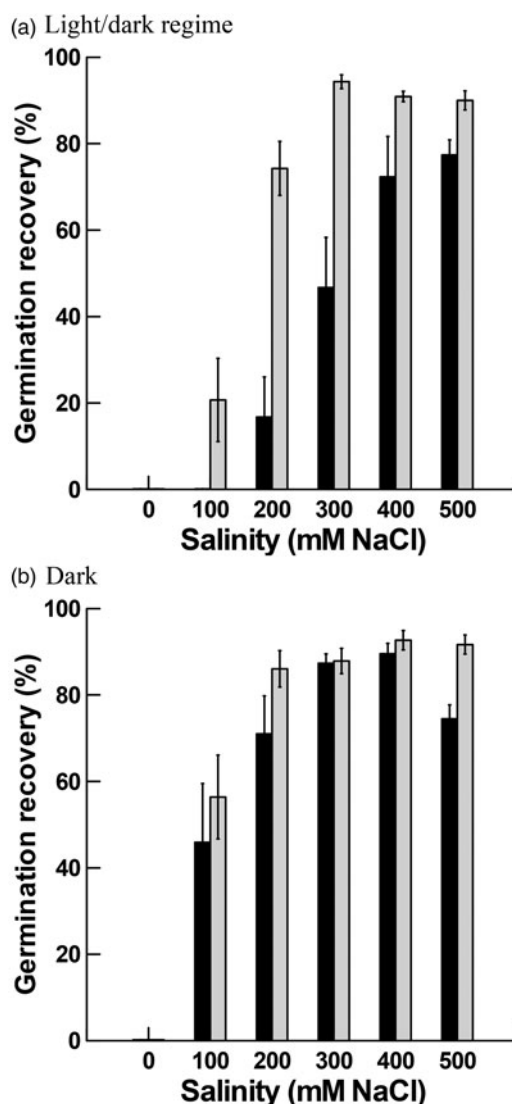


**Fig. 2.** Effects of maternal salinity, and salinity and temperature of incubation on germination rate index (mean  $\pm$  SE) of *Suaeda vermiculata* seeds. Dark and light bars are for seeds of non-saline and saline habitats, respectively.

saline habitat in the different salinities, compared with those from the saline habitats, disappeared with the greater recovery observed for seeds of saline habitat (data not shown).

### Discussion

Among the important adaptive features that distinguish seeds of halophytes from those of glycophytes is their ability to delay



**Fig. 3.** Effects of maternal salinity, salinity and light of incubation on germination recovery (mean  $\pm$  SE) of *Suaeda vermiculata* seeds. Dark and light bars are for seeds of non-saline and saline habitats, respectively.

their germination under salinity stress until alleviation of such stress (Khan and Gul, 2006). An important consequence of the germination recovery upon alleviation of salt stress is to determine the salinity level at the time of seedling development, which is one of the most sensitive stages in the life cycle of halophytes (Pujol *et al.*, 2000). Therefore, the amount of precipitation that is needed to dilute soil salinity would determine the timing of seed germination of halophytes. *Suaeda vermiculata* seeds of the saline habitat failed to germinate in 400 and 500 mM NaCl, indicating that they postpone their germination until salinity is diluted through rainfall. The very fast recovery of most of the non-germinated seeds of the saline habitat when transferred from the saline solutions to distilled water is an ecological adaptation for survival in saline soils. In *S. vermiculata* almost all the non-germinated seeds recovered within 2 days after being transferred to distilled water.

Temperature is a crucial factor determining germination timing of non-dormant seeds in most species. Temperature can interact with salinity to affect seed germination. Although higher

salinity may inhibit germination, the detrimental effect of salinity is generally reduced at optimal germination temperatures (De Villiers *et al.*, 1994; Aiazzi *et al.*, 2002). In our study, there was no significant difference in final germination of *S. vermiculata* between the different temperatures for both seeds from the saline and non-saline habitats. In saline solution, however, germination decreased with the increase in both temperature and salinity. Salinity–temperature interaction may have significant ecological implications in terms of timing of germination under field conditions (El-Keblawy and Bhatt, 2015). The higher germination of *S. vermiculata* in the higher salinities (400 and 500 mM NaCl) at lower temperatures (15/25°C) indicates a higher probability of seedling survival if germination occurred early in the growing season (e.g. December), when temperatures are low and chance of rainfall is higher. The average minimum and maximum temperatures in December are around 15 and 25°C, respectively (Böer, 1997). However, the chance of seedling establishment would be much lower if germination occurred at higher temperatures by the end of the growing season, when there is almost no rainfall to dilute soil salinity. In addition, germination reduction at higher temperatures has been attributed to increased evaporation of moisture, which in turn increases salt concentration by capillary movement (Khan and Ungar, 1997). It has been reported that the changes in fluidity and permeability of cell membranes occur at extreme temperatures (Raison, 1986). The high temperatures can result in loss of the semi-permeability of the plasma membrane, which leads to an increase in the amount of electrolyte leakage.

It has been reported that salt tolerance during the germination stage depends on the interaction between temperature and light in some halophytes (De Villiers *et al.*, 1994; El-Keblawy and Al-Rawai, 2005; El-Keblawy *et al.*, 2007). Our results indicate that the salt tolerance of *S. vermiculata* depended on light and temperature of incubation of seeds from both saline and non-saline habitats. There was no significant difference between germination in dark and light of seeds of both saline and non-saline habitats in the lower salinities (0 and 100 mM NaCl). At higher salinities, however, germination was significantly reduced in dark than in light, especially at the higher temperatures (Fig. 1). Similarly, in *Limonium stocksii*, little difference between germination in light was observed at lower salinities, but almost no germination occurred in darkness at higher salinities (Zia and Khan, 2004). In addition, seeds of *Crithmum maritimum* germinated well in light and dark in distilled water, but germination was almost inhibited in darkness in saline solution (Atia *et al.*, 2009).

The variation in the ability of plants of different populations to adapt to local environmental stresses can be genetically fixed within a population (Moriuchi *et al.*, 2016), and may be triggered by maternal environmental effects and offspring phenotypic plasticity (Herman and Sultan, 2011). The local adaptation level depends on a balance between local selective pressures and regional dispersal processes. A negative association has been expected between dispersal and local adaptation (Galloway and Etterson, 2009). The presence of multiple generations of *S. vermiculata* that has limited seed dispersed, within a single environment, would increase the likelihood of population differentiation between saline and non-saline environments (Moriuchi *et al.*, 2016). However, despite the fact that seeds from the saline habitat matured under higher salinity stress, they tolerated less salinity during the germination stage, compared with seeds matured in the non-saline habitat (Fig. 1).

## Conclusions

*Suaeda vermiculata* seeds of the saline habitat attained significantly lower germination in higher salt solutions compared with those of non-saline habitat. The high viability of the non-germinated seeds of the saline habitat indicates that they postpone their germination until the onset of the favourable conditions for seedling establishment, which usually occurs after effective rainfall. Almost all the seeds that failed to germinate in saline solutions germinated after transfer to distilled water. However, as this species has limited seed dispersal, the ecological significance for the greater germination of non-saline habitat seeds at the higher salinity levels is not clear. More research to define the maternal and epigenetic effects of transgenerational changes in germination behaviour is needed.

**Acknowledgements.** The authors would like to thank Mrs Attiat Elnaggar, Alexandria University, for her help in data collection.

**Financial support.** This work was partially supported through a grant from the Research Office of University of Sharjah that supported the Environmental and Chemical Biology Research Group (grant no. 150404).

**Supplementary material.** To view supplementary material for this article, please visit <https://doi.org/10.1017/S0960258518000144>

## References

- Aiazzi MT *et al.* (2002) Effects of salinity and temperature on the germination and early seedling growth of *Atriplex cordobensis* Gandoger et Stuckert (Chenopodiaceae). *Seed Science and Technology* **30**, 329–338.
- Atia A *et al.* (2009) Interactive effects of salinity, nitrate, light, and seed weight on the germination of the halophyte *Crithmum maritimum*. *Acta Biologica Hungarica* **60**, 433–439.
- Benech-Arnold RL *et al.* (2000) Environmental control of dormancy in weed seed banks in soil. *Field Crops Research* **67**, 105–122.
- Böer B (1997) An introduction to the climate of the United Arab Emirates. *Journal of Arid Environments* **35**, 3–16.
- Bradbeer JW (1998) *Seed Dormancy and Germination*. New York: Chapman and Hall.
- Cushman JC (2001) Osmoregulation in plants: implications for agriculture. *American Zoologist* **41**, 758–769.
- Dahnke WC and Whitney DA (1988) Measurement of soil salinity. In Recommended Chemical Soil Test Procedures for the North Central Region. North Central Regional Publication 221. *North Dakota Agricultural Experiment Station Bulletin* **499**, 32–34.
- De Villiers AJ *et al.* (1994) Germination of three Namaqualand pioneer species, as influenced by salinity, temperature and light. *Seed Science and Technology* **22**, 427–433.
- Donohue K (2009) Completing the cycle: maternal effects as the missing link in plant life histories. *Philosophical Transactions of the Royal Society B: Biological Sciences* **364**, 1059–1074.
- Donohue K and Schmitt J (1998) Maternal environmental effects in plants: adaptive plasticity. In Mousseau TA and Fox CW (eds), *Maternal Effects as Adaptations*. New York: Oxford University Press, pp. 137–158.
- El-Keblawy A *et al.* (2007) Salinity, temperature and light affect germination of *Salsola imbricata*. *Seed Science and Technology* **35**, 272–281.
- El-Keblawy A and Al-Rawai A (2005) Effects of salinity, temperature and light on germination of invasive *Prosopis juliflora* (SW.) D.C. *Journal of Arid Environments* **61**, 555–565.
- El-Keblawy A and Bhatt A (2015) Aerial seed bank affects germination behaviour of two small seeded halophytes in the Arabian deserts. *Journal of Arid Environments* **115**, 10–17.
- El-Keblawy A and Gairola S (2017) Dormancy regulating chemicals alleviate innate seed dormancy and promote germination of desert annuals. *Journal of Plant Growth Regulation* **36**, 300–311.

- El-Keblawy A, Gairola S and Bhatt A** (2016) Maternal salinity environment affects salt tolerance during germination in *Anabasis setifera*: a facultative desert halophyte. *Journal of Arid Land* **8**, 254–263.
- El-Keblawy A et al.** (2017a) Effects of maternal salinity on salt tolerance during germination of *Suaeda aegyptiaca*: a facultative halophyte in the Arab Gulf desert. *Plant Species Biology* **32**, 45–53.
- El-Keblawy A et al.** (2017b) Effect of maturation time on dormancy and germination of *Citrullus colocynthis* (Cucurbitaceae) seeds from the Arabian Hyper-arid Deserts. *BMC Plant Biology* **17**, 263. doi: 10.1186/s12870-017-1209-x
- El-Keblawy A et al.** (1996) Maternal effect on progeny in *Thymelaea hirsuta*. *New Phytologist* **132**, 77–85.
- Fenner M** (1991) The effects of the parent environment on seed germinability. *Seed Science Research* **1**, 75–84.
- Galloway LF** (2005) Maternal effects provide phenotypic adaptation to local environmental conditions. *New Phytologist* **166**, 93–100.
- Galloway LF and Etterson JR** (2009) Plasticity to canopy shade in a monocarpic herb: within- and between-generation effects. *New Phytologist* **182**, 1003–1012.
- Grattan SR and Grieve CM** (1998) Salinity–mineral nutrient relations in horticultural crops. *Scientia Horticulturae* **78**, 127–157.
- Greenway H and Munns R** (1980) Mechanisms of salt tolerance in non-halophytes. *Annual Review of Plant Physiology* **31**, 149–190.
- Gul B et al.** (2013) Germination strategies of halophyte seeds under salinity. *Environmental and Experimental Botany* **92**, 4–18.
- Guterman Y** (2000) Maternal effects on seeds during development. In Fenner M (ed), *Seeds: the Ecology of Regeneration in Plant Communities*, 2nd edition. Wallingford: CABI Publishing, pp. 59–84.
- Hameed A et al.** (2014) Salinity inhibits seed germination of perennial halophytes *Limonium stocksii* and *Suaeda fruticosa* by reducing water uptake and ascorbate dependent antioxidant system. *Environmental and Experimental Botany* **107**, 32–38.
- Herman JJ and Sultan SE** (2011) Adaptive transgenerational plasticity in plants: case studies, mechanisms, and implications for natural populations. *Frontiers in Plant Science* **2**, 102.
- Holeski LM, Jander G and Agrawal AA** (2012) Transgenerational defense induction and epigenetic inheritance in plants. *Trends in Ecology & Evolution* **27**, 618–626.
- Jones IF and Hall MA** (1979) Studies on the seed requirement for carbon dioxide and ethylene for germination of *Spergula arvensis* seeds. *Plant Science Letters* **16**, 87–93.
- Khan MA and Gul B** (2006) Halophyte seed germination. In Khan MA and Weber DJ (eds), *Ecophysiology of High Salinity Tolerant Plants*. Karachi-75270, Pakistan: Department of Botany, University of Karachi, pp. 11–30.
- Khan M and Ungar I** (1997) Effects of thermoperiod on recovery of seed germination of halophytes from saline conditions. *American Journal of Botany* **84**, 279–279.
- Kranner I, and Seal CE** (2013) Salt stress, signalling and redox control in seeds. *Functional Plant Biology* **40**, 848–859.
- Maruyama C et al.** (2016) Effects of population site and maternal drought on establishment physiology in *Impatiens capensis* meerb. (Balsaminaceae). *Rhodora* **118**, 32–45.
- Merabtene T, Siddique M and Shanableh A** (2016) Assessment of seasonal and annual rainfall trends and variability in Sharjah City, UAE. *Advances in Meteorology*, article ID 6206238.
- Milberg P, Andersson L and Thompson K** (2000) Large-seeded species are less dependent on light for germination than small-seeded ones. *Seed Science Research* **10**, 99–104.
- Moriuchi KS et al.** (2016) Salinity adaptation and the contribution of parental environmental effects in *Medicago truncatula*. *PLoS One* **11**, e0150350.
- Pujol JA, Calvo JF and Ramirez-Diaz L** (2000) Recovery of germination from different osmotic conditions by four halophytes from southeastern Spain. *Annals of Botany* **85**, 279–286.
- Qu XX et al.** (2008) Effect of temperature, light and salinity on seed germination and radicle growth of the geographically widespread halophyte shrub *Halogetonum strobilaceum*. *Annals of Botany* **101**, 293–299.
- Raison JK** (1986) Alterations in the physical properties and thermal response of membrane lipids: correlations with acclimation to chilling and high temperature. In St John JB, Berlin E and Jackson PC (eds), *Frontiers of Membrane Research in Agriculture*. Totowa, NJ: Rowman and Allanheld, pp. 383–401.
- Rossiter MC** (1996) Incidence and consequences of inherited environmental effects. *Annual Review of Ecology and Systematics* **27**, 451–476.
- Rossiter MC** (1998) The role of environmental variation in parental effects expression. In Mousseau TA and Fox CW (eds), *Maternal Effects as Adaptations*. Oxford, UK: Oxford University Press, pp. 112–134.
- Ungar IA** (1995) Seed germination and seed-bank ecology in halophytes. In Kigel J and Galili G (eds), *Seed Development and Germination*. New York: Marcel Dekker, pp. 599–628.
- Wulff RD** (1995) Environmental maternal effects on seed quality and germination. In Kigel J and Galili G (eds), *Seed Development and Germination*. New York: Marcel Dekker, pp. 491–505.
- Zia S and Khan MA** (2004) Effect of light, salinity, and temperature on seed germination of *Limonium stocksii*. *Canadian Journal of Botany* **82**, 151–157.